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Sediment organic carbon integrates changing environmental conditions to predict benthic assemblages in shallow Arctic seas

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Abstract

1. In marine spatial planning, conserving adequate habitats and the food webs they support requires delineating habitats and projecting future trends. For bottom-feeding marine birds and mammals, repeated benthic sampling over large areas to document changes and to develop predictive models of prey dispersion is quite costly. More easily monitored variables that relate strongly to the biomass and structure of benthic assemblages, and are more readily predicted from physical models of climate change, would facilitate planning efforts.

2. The organic carbon (OC) content of sediments integrates diverse physical and biotic processes, and can be less variable over time than primary production, salinity, temperature, or position of water masses. Sediment OC further subsumes inputs at the base of food webs that can limit carbon flows to higher taxa.

3. For the northern Bering Sea, this study explored the utility of sediment OC as a predictor of benthic assemblage types. Cluster analysis and multi-dimensional scaling distinguished three main types along a gradient of sediment OC.

4. The assemblage for highest sediment OC had a much greater biomass of brittlestars, diverse marine worms, and two mid-sized, thinner-shelled bivalves selected as prey by diving sea ducks. The assemblage for lowest sediment OC lacked brittlestars, had a much greater biomass of amphipods sought by gray whales (*Eschrichtius robustus*), and had a much higher biomass of two often larger or thicker-shelled bivalves commonly targeted by walruses (*Odobenus rosmarus*). Areas of exceptionally low sediment OC tended towards dominance by sand dollars with low foraging value.

5. Our study shows that sediment OC has promise as a proxy for monitoring and predicting changes in important prey assemblages in a given region. Models that link predicted hydrographic patterns to lateral advection of phytodetritus, and the resulting sediment OC, may further allow the use of physical climate models to project the future dispersion of benthic habitats for endothermic predators.

KEYWORDS

benthos, climate change, habitat mapping, invertebrate assemblages, marine spatial planning, ocean, phytodetritus, sediment organic matter

1 | INTRODUCTION

With shifting climate and increasing human impacts, long-term conservation planning requires delineating and projecting changes in habitats and the food webs they support (Brigham, 2011; Carroll, Dunk, & Moilanens, 2010; Gormley, Porter, Bell, Hull, & Sanderson, 2013; Hole et al., 2011). In the shallow seas of the Amerasian Arctic, much of the food-web biomass is benthic, and a number of endothermic top predators [sea ducks, bearded seals (*Erignathus barbatus* Erxleben), walruses (*Odobenus rosmarus* Linnaeus), and gray whales (*Eschrichtius robustus* Lilljeborg)] feed mainly or entirely on benthic fish or invertebrates (Brower, Ferguson, Schonberg, Jewett, & Clarke, 2017; Crawford, Quakenbush, & Citta, 2015; Lovvorn et al., 2014; Sheffield & Grebmeier, 2009). Developing cost-effective ways to monitor and predict changes in the dispersion of different prey assemblages is key to conserving adequate habitats for these predators into the future (Pace, Carpenter, & Cole, 2015; Reiss et al., 2015; Weinert et al., 2016). For the northern Bering Sea, this study explored the utility of sediment organic carbon as a proxy indicator of shifts in prey assemblages, and as a potential variable for linking climatic physical forcing to spatial patterns of food-web response.

Large areas of soft sediments on continental shelves of the Amerasian Arctic are dominated by deposit feeders and filter feeders. These organisms feed mostly on settled microalgae (ice algae and phytoplankton), and especially on bacteria that consume algal-derived organic matter (Lovvorn, Jacob, et al., 2015; McTigue & Dunton, 2014; North et al., 2014). As a result, spatial patterns of benthic taxa are often strongly related to the organic carbon (OC) content of the sediments (Blanchard & Feder, 2014; Carroll & Ambrose, 2012; Denisenko, Denisenko, Lehtonen, Andersin, & Laine, 2003; Grebmeier, Cooper, Feder, & Sirenko, 2006). Local patch structure of sediment OC is in turn affected by lateral advection of settled phytodetritus by wind-related currents (Lovvorn et al., 2013; Puls & Sundermann, 1990; Rutgers van der Loeff, Meyer, Rudels, & Rachor, 2002). Along with changes in the strength and direction of prevailing winds, the dispersion of sediment OC and associated benthic assemblages can change over a few years to decades (Cooper et al., 2002, 2012; Grebmeier et al., 2015; Lovvorn et al., 2014).

If assemblages are characterized along a gradient of existing conditions, and that gradient reflects changes expected with climate trends, then a space-for-time analysis can indicate the likely trajectory of assemblages with changing climate (Pace et al., 2015; Weinert et al., 2016). Regular field sampling to document temporal shifts in the patch structure of benthic feeding sites for endothermic predators over large areas is often too expensive in the long term. However, recent efforts to model and map benthic assemblages based on more readily measured proxy variables have allowed important advances in marine spatial planning at much reduced cost (Gonzalez-Mirelis & Buhl-Mortensen, 2015; McArthur et al., 2010; McHenry, Steneck, & Brady, 2017). Variables that can be sampled more regularly or opportunistically, or can be directly predicted from physical models, would greatly facilitate the scaling down from climate models to local biological response (Ådlandsvik, 2008; Brown et al., 2013; Myksvoll, Sandvik, Skar∂hamar, & Sundby, 2012).

Sediment OC integrates many processes that affect benthic assemblages. Sediment OC subsumes phytoplankton production and the lateral advection of settled phytodetritus, as well as fluctuating hydrography which also mediates larval dispersal and settlement (Hunt, Fugate, & Chant, 2009; Puls & Sundermann, 1990; Rosenberg, 1995). As both variables are related to current speed, sediment OC is typically strongly correlated with sediment grain size, another key influence on benthic assemblages (Feder et al., 1994; Feder, Jewett, & Blanchard, 2007; Grebmeier et al., 2006, 2015). However, sediment OC encompasses a broader array of physical and biological effects (Gray & Elliott, 2009). Both grain size and OC content affect sediment porosity and exchange of pore water and dissolved oxygen; however, levels of OC can cause further large variations in sediment hydraulic conductivity and oxygen demand. These variables in turn result in vertical and horizontal gradients of redox conditions that favour different bacteria, geochemical processes, rates of organic degradation, and meiofauna and macrofauna. The smaller particles that typically occur with increased sediment OC can clog the gills of filter feeders, reducing their abundance relative to deposit feeders (Newcombe & MacDonald, 1991). Finally, sediment OC is proportional to food inputs at the base of food webs, which can limit the energy transmitted to higher trophic levels, thereby altering assemblage structure and species interactions (Lovvorn, Jacob, et al., 2015; McTigue & Dunton, 2014; North et al., 2014; Rosenberg, 1995).

Abiotic variables such as bottom temperature, salinity, and the nutrient content of overlying water masses can also be important covariates of assemblage types (Pisareva et al., 2015; Ravelo, Konar, Trefry, & Grebmeier, 2014; Schonberg, Clarke, & Dunton, 2014). However, in shallow areas these factors often fluctuate widely, both seasonally and annually (Danielson, Eisner, Weingartner, & Aagaard, 2011; Danielson, Hedstrom, Aagaard, Weingartner, & Curchitser, 2012), thus requiring continuous monitoring by in situ instruments that in Arctic coastal areas can be vulnerable to ice damage. On shallow shelves with low depth gradients, water depth affects benthic assemblages mostly indirectly by affecting other variables (McArthur et al., 2010). Primary production in the water column is also important, as the accumulation of that production on the sea floor fuels benthic assemblages. However, the inability of satellite sensors to penetrate to the depth of the chlorophyll maximum, and the lateral advection of settled phytodetritus, can confound spatial correlations of water-column production measurements with underlying sediment OC and food supply (Carroll & Ambrose, 2012; Lovvorn et al., 2013; Lovvorn, Jacob, et al., 2015).

If shifts in benthic assemblages can be predicted from changes in sediment OC (Lovvorn et al., 2016), there is an opportunity to infer the likely persistence of prey assemblages based on more frequent field surveys of this more easily measured variable. Such relationships might also aid in projecting climate-driven assemblage changes based on physical models of the lateral transport of settled phytodetritus and organic sediments (Ådlandsvik, 2008; Danielson et al., 2012; Myksvoll et al., 2012; Puls & Sundermann, 1990; Weinert et al., 2016). In this analysis, the utility of sediment OC for predicting shifts in benthic fish and macroinvertebrate assemblages was examined over a large area of the northern Bering Sea.

2 | METHODS

2.1 | Study area, sampling stations, and sample treatment

Data analysed in this paper were also used in the food-web modelling of Lovvorn, Jacob, et al. (2015) and Lovvorn et al. (2016). Benthic organisms and sediment organic matter were sampled in the northern Bering Sea from 18 May to 12 June 2007 from the US Coast Guard icebreaker *Healy* (Figure 1). For much or all of the year in our study area, bottom water temperatures are <1°C in the Chirikov Basin north of St. Lawrence Island, and < 0°C south of the island. Pack ice covers these areas for 5–6 months per year. Water depths at the sampling stations were 35–52 m in the Chirikov sector, and 30–96 m in the southern sector. The southern study area is generally dominated by a single water mass (Bering Shelf Water). The Chirikov Basin includes three northward-flowing water masses positioned from west to east (Anadyr Water, Bering Shelf Water, and Alaska Coastal Water), with fronts between them shifting seasonally and even by tens of kilometres in only a few days (Gawarkiewicz, Haney, & Caruso,

1994). Infauna were sampled with a 0.1-m² van Veen grab, and organisms retained by a 1-mm sieve were identified. Epifauna were sampled with a 4-m beam trawl (with 1.9-cm Square mesh). Analyses here include only stations where both grab and trawl samples were collected. All biomasses are expressed as g C (conversion factors can be found in the supplementary material provided by Lovvorn, Jacob, et al., 2015).

At each station (Figure 1), standing stocks of chlorophyll *a* and total organic carbon were measured in the top 1 cm of sediments (Cooper et al., 2012). Chlorophyll *a* (chl *a*) was converted to g C of fresh microalgae by the ratio 34 g C (g chl *a*)$^{-1}$ (details of data and calculations can be found in the supplementary material for Lovvorn, Jacob, et al., 2015). Some chlorophyll may persist in sediments for long periods (Pirtle-Levy, Grebmeier, Cooper, & Larsen, 2009), and would be included in 'fresh' microalgae. However, the intent here was to separate intact algal cells containing viable chlorophyll from the more degraded pool of sediment organic matter. The latter organic pool reflects net erosion and deposition of sediments throughout the year, and its regeneration in bacteria appears to provide the primary direct input to detritus-based food webs in this
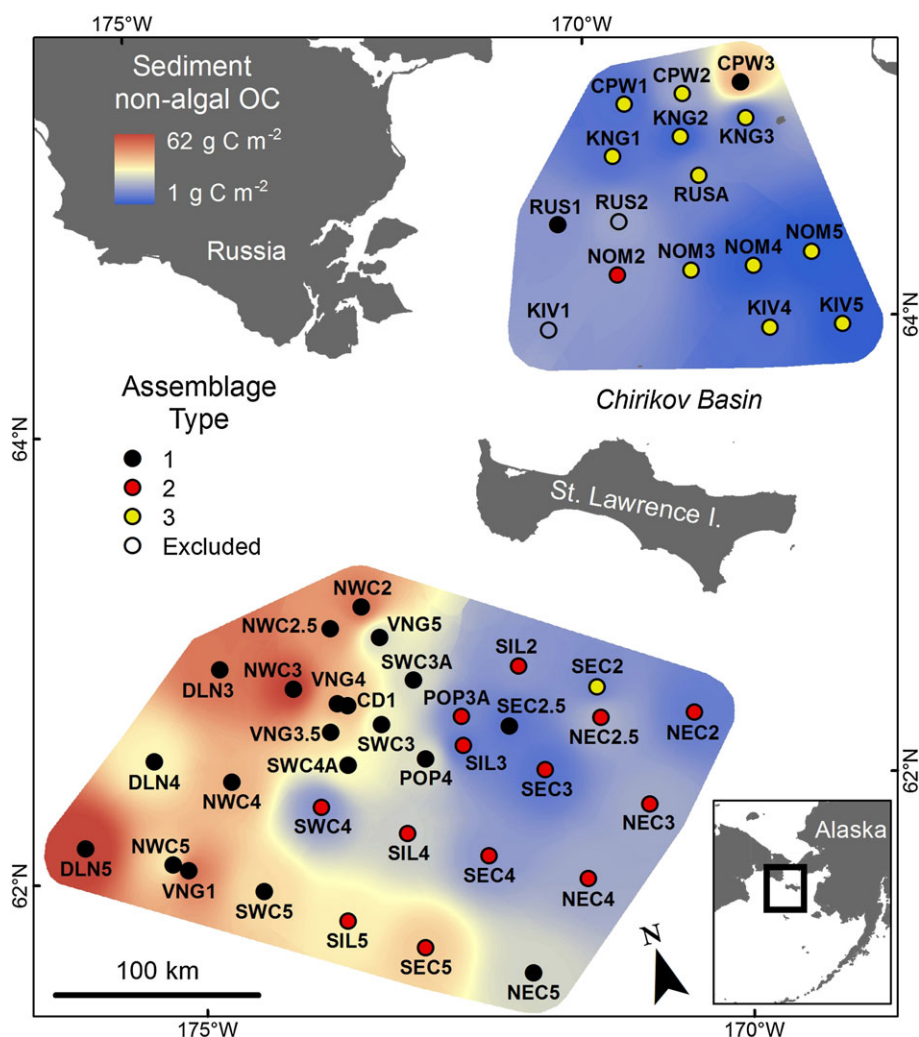

FIGURE 1 Stations for grab and trawl samples, and interpolation among stations of sediment non-algal organic carbon (OC, g C m^{-2}), in the northern Bering Sea in May–June 2007. Assemblage types identified by cluster analysis and non-metric multidimensional scaling (MDS) are indicated by circles of different colours

region. The biomass of non-algal sediment organic carbon (OC) was calculated by subtracting the biomass of fresh microalgae from total OC. X-ray images of cores show that most infauna occurs within the top 5 cm (Grebmeier & McRoy, 1989), in which the sediments are typically well mixed (Pirtle-Levy et al., 2009). Thus, OC measurements in the top 1 cm are representative of conditions experienced by most benthic macrofauna. Sand, silt, and clay fractions of the top 1 cm of sediments were determined by wet and dry sieving.

Especially on shallow continental shelves, phytodetritus settling from the water column is often resuspended and redistributed to different sites by wind-driven currents (Lampitt, 1985; Lovvorn et al., 2013; Puls & Sundermann, 1990). This transport results in transient variations in fresh microalgae deposited at a particular location. Moreover, a number of studies have concluded that despite major seasonal pulses of fresh microalgae, deposit feeders often depend strongly on a longer-term 'food bank' of sediment organic matter that is probably regenerated by bacterial intermediates (Byrén, Ejdung, & Elmgren, 2006; Josefson, Forbes, & Rosenberg, 2002; McTigue & Dunton, 2014; Mincks, Smith, Jeffreys, & Sumida, 2008; North et al., 2014; Rudnick, 1989). Thus, in this study, the non-algal (excluding fresh microalgae) OC content of sediments was used as the best measure of the net input of organic matter over longer periods at a given site.

2.2 | Data analysis

For the analyses in this paper, abundant bivalve taxa were separated by species or genus, whereas polychaetes and amphipods were not. Reports on the diets of benthic-feeding eider ducks, bearded seals, and walruses have often not distinguished taxa of amphipods or polychaetes, whereas bivalves have usually been identified to species level (Crawford et al., 2015 and references therein; Lovvorn, Richman, Grebmeier, & Cooper, 2003; Lovvorn et al., 2014; Merkel, Mosbech, Jamieson, & Falk, 2007; Sheffield & Grebmeier, 2009). Moreover, the spectacled eiders (*Somateria fischeri* Brandt) in our study area, which ate only bivalves, selected certain species and sizes, apparently because of differing intake rates and energy content, as prey (Lovvorn et al., 2003; Richman & Lovvorn, 2003). Given our goal of identifying major trophic assemblages with regard to endothermic predators, the trophic functions of polychaete detritivores, polychaete carnivores, and amphipods were assumed to remain similar within those groups among stations (Lovvorn, Jacob, et al., 2015).

Biomasses were square-root transformed before calculating Bray–Curtis dissimilarities among each taxon. This transformation is justified by the fact that the biomass was often dominated by a few abundant taxa of infauna, and information on assemblage structure provided by less abundant taxa would be under-used without transformation (Clarke, Gorley, Somerfield, & Warwick, 2014). Using PRIMER 7 (Clarke et al., 2014), both cluster analysis and non-metric multidimensional scaling (MDS) were used to analyse assemblages. Differences among assemblages identified by cluster analysis and MDS were examined a posteriori with SIMPROF (similarity profile) tests;

ANOSIM (analysis of similarity) tests were not performed as the groups were not identified a priori (Clarke et al., 2014).

3 | RESULTS

3.1 | Assemblage types and relation to sediment OC

Both cluster analysis and MDS divided the sampling stations into three main assemblage types (Figures 2, 3; SIMPROF test, $P < 0.05$). With some exceptions, these assemblage types corresponded to three geographic sectors of the study area: types 1 and 2 in the western and eastern portions south of St. Lawrence Island, respectively, and type 3 in the Chirikov Basin north of the island (Figure 1). The moderately high two-dimensional stress value of 0.19 (Figure 3) reflects some difficulty in representing the Bray–Curtis dissimilarity rankings in a two-dimensional plot. Two stations in the Chirikov Basin (KIV1 and RUS2) clustered individually, and were omitted from further analyses. KIV1, which experiences exceptionally high flows from the Anadyr Current as it streams northwards into the Chirikov Basin, was dominated by the sand dollar *Echinarachnius parma* Gray and a very large biomass of the filter-feeding bivalve *Astarte borealis* Schumacher (note that after first mention of Latin names in the text, species lacking standard common names will be referred to by genus only). RUS2 had a biomass of polychaete detritivores (mostly Ampharetidae) that was an order of magnitude higher than found at any other station, and an unusually high biomass of large shorthorn sculpins (*Myoxocephalus scorpius* Linnaeus), whose guts were filled with these polychaetes.

Multidimensional scaling (MDS) showed a strong association of the three main assemblage types to a gradient of non-algal OC content of sediments (excluding recently settled, potentially transient microalgae; Figure 4). Without exception, groupings of assemblages at different stations relative to the percentage of silt and clay were the same as for sediment OC, indicating that sediment OC subsumed most effects of sediment grain size. (Non-algal sediment OC was strongly correlated with the percentage of silt and clay: $r^2 = 0.73$, $P < 0.001$, $n = 49$ stations.) Non-algal sediment OC differed significantly between the three main assemblage types (Bonferroni pairwise comparisons on ranked data, $P < 0.05$; Figure 5).

3.2 | Structure of assemblage types

The structure of different assemblage types was compared in terms of relative biomasses among taxa (Figure 6). Square roots were used to increase the relative information provided for taxa with lower biomasses, and to correspond to values used in the cluster and MDS analyses. Among the three main assemblage types, amphipods had far greater biomass in type 3, whereas the mid-sized bivalves *Nuculana radiata* Krause and *Ennucula tenuis* Montagu had much higher biomass in type 1 (Figure 6). There was also a shift in fish dominance from flatfish in types 1 and 2 to large sculpins in type 3. The non-polychaete worms – Priapulidae, Sipuncula, and Nemertea – had much higher biomass in type 1 than in the other types, as did the brittlestar *Ophiura sarsi* Lütken, which along with Priapulidae did not occur in type 3. Assemblage type 2
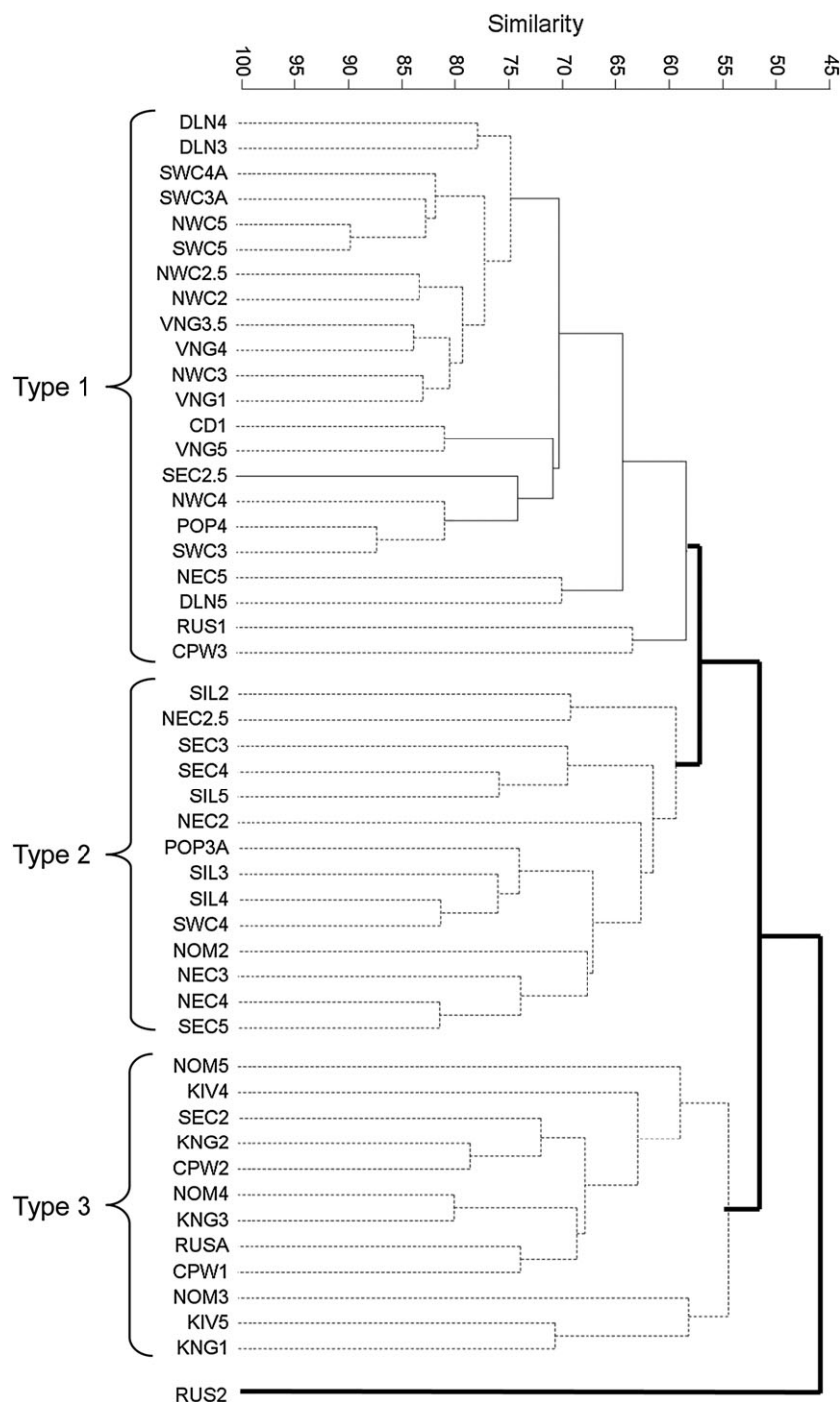
FIGURE 2 Cluster analysis of sampling stations (Figure 1) based on Bray–Curtis dissimilarities among the square roots of carbon masses (g C m^{-2}) of benthic taxa. Linkage levels indicate percentage similarity. Clusters that differ significantly are linked by bold solid lines (SIMPROF tests, $P < 0.05$), and represent the major assemblage types recognized in this paper

exhibited consistently intermediate biomasses, except for the lack of the bivalves *Astarte* and *Serripes groenlandicus* Mohr.

4 | DISCUSSION

4.1 | Sediment organic carbon and assemblage patterns

Our analyses indicate that variations in the taxonomic and biomass structure of benthic assemblages in the northern Bering Sea are closely related to factors associated with the longer-term OC content of sediments (excluding recently settled, potentially transient microalgae). Over a gradient of

decreasing sediment OC from assemblage type 1 to type 3, changes included:

- Large increase in filter-feeding amphipods
- Large decreases in the deposit-feeding bivalves *Nuculana* and *Ennucula*, with increased biomasses of the filter-feeding bivalves *Serripes* and *Astarte*
- Large decreases in deposit-feeding Sipunculid and predatory Nemertean worms, and disappearance of predatory Priapulid worms
- Decrease in deposit-feeding or scavenging brittlestars from abundant to virtually absent, and appearance of sand dollars at some stations
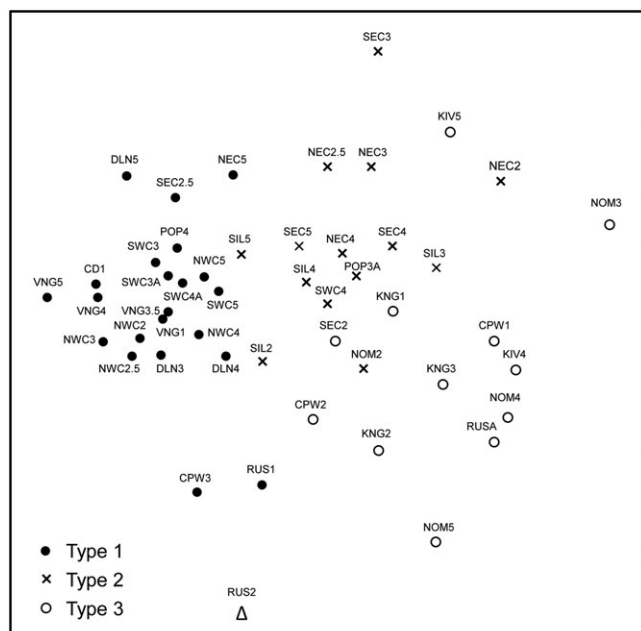
FIGURE 3 Non-metric multidimensional scaling (MDS) plot of sampling stations (Figure 1) based on Bray–Curtis dissimilarities among the square roots of carbon mass (g C m^{-2}) of benthic taxa. The two-dimensional stress value was 0.19. The three main assemblage types differed significantly from each other and from the assemblage at station RUS2 (SIMPROF test, $P < 0.05$). Station KIV1 (Figure 1) also clustered individually, and was far off the scale of this diagram
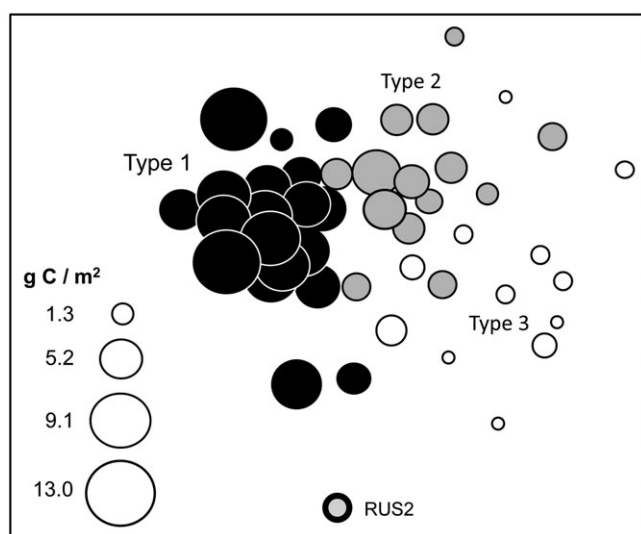

FIGURE 4 Non-metric multidimensional scaling (MDS) plot of sampling stations based on benthic assemblages (square root of g C m^{-2}), where the sizes of bubbles are proportional to the non-algal sediment organic carbon (g C m^{-2}) at each station (two-dimensional stress = 0.19). Assemblage types 1 (black), 2 (gray), and 3 (white) differed significantly (Figure 3), as did their non-algal (excluding fresh microalgae) sediment organic content (Figure 5)
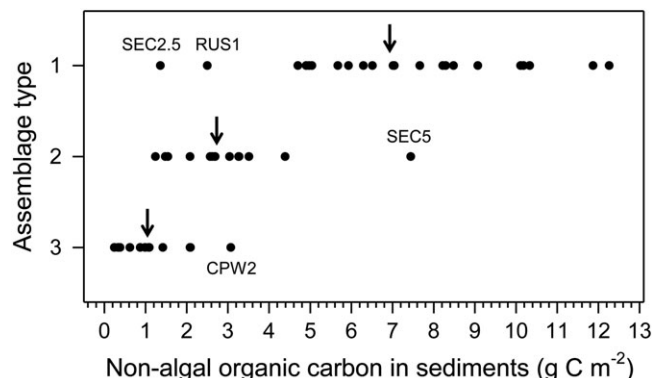
- Decrease in flatfish and increase in sculpins. These changes represent a trend from mainly deposit-feeding to more filter-feeding consumers and their predators, as would be expected with reduced OC of sediments.


FIGURE 5 Non-algal organic carbon (excluding recently settled, still-transient microalgae) in the top 1 cm of sediments at sampling stations with different assemblage types. Arrows indicate median values. Stations that overlap medians for other assemblage types are annotated (station locations in Figure 1). The non-algal organic carbon content of sediments differed among assemblage types (Bonferroni pairwise comparisons on ranked data, $P < 0.05$)

There are no major currents that traverse the study area south of St. Lawrence Island. However, the Anadyr Current, the major current flowing from the Pacific Ocean north towards the Arctic Ocean, is highly variable in strength and position in the south-western portion of the Chirikov Basin (Clement, Maslowski, Cooper, Grebmeier, & Walczowski, 2005; Gawarkiewicz et al., 1994). In that area, surface winds can displace the east–west position of the front between the Anadyr Current and Bering Shelf water by tens of kilometres in only 2–4 days (Gawarkiewicz et al., 1994). Such shifts can substantially alter spatial patterns of erosive versus depositional forces, settling of planktonic larvae, and conditions for species sorting (cf. Kolts, Lovvorn, North, & Janout, 2015). As a result, patterns of assemblage types in the south-west region of the Chirikov Basin are more variable and somewhat idiosyncratic compared with the rest of our Chirikov study area (Figure 1). Higher spatial and temporal variance and delayed recovery from disturbances are believed to anticipate major shifts between assemblage types (Litzow, Mueter, & Urban, 2013; Pace et al., 2015). Thus, assemblages in the south-west Chirikov Basin may be more susceptible to state changes, especially in light of the heavy predation on amphipods and associated benthic disturbance by gray whales in this area (Clark & Johnston, 2009; Coyle, Bluhm, Konar, Blanchard, & Highsmith, 2007; Oliver & Slattery, 1985).

On the shallow and often stormy northern Bering Sea shelf, high levels of stochastic environmental disturbance might result in variable assemblage structure with little effect of species interactions (Harris, 2012; Harris & Hughes, 2012). Based on spatial patterns of food web structure and function, Lovvorn, Jacob, et al. (2015) suggested that assemblages throughout the study area were strongly influenced by recruitment events after abiotic disturbances, and that interactions among species had less influence than priority effects of variable recolonization. However, subsequent food-web simulations indicated that certain deposit-feeding taxa respond more strongly to changes in sediment OC and the resulting production of bacterial foods, an effect that is transmitted to higher trophic levels (Lovvorn et al., 2016). In both computer simulations and field samples, the primary consequences of decreased sediment OC included the loss of several
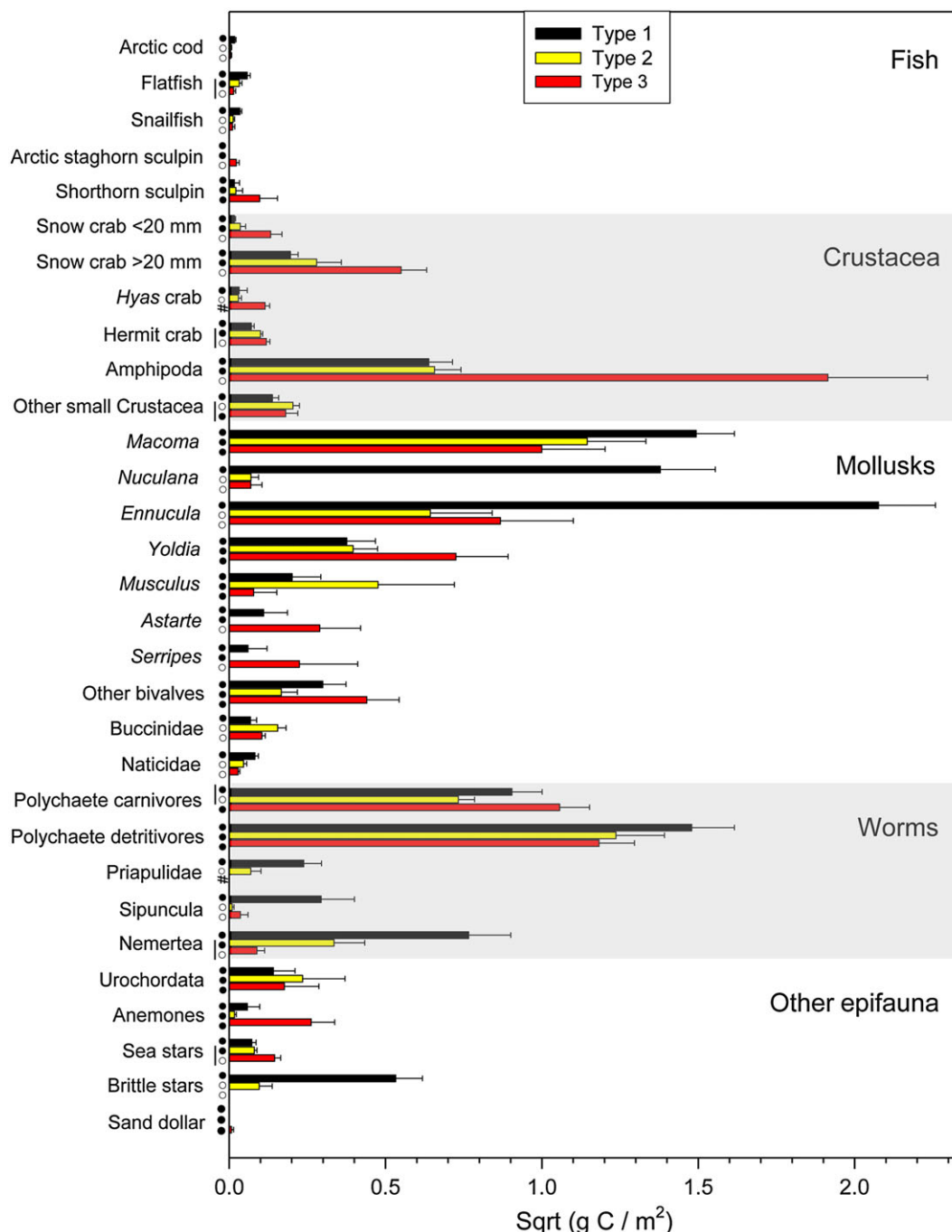
FIGURE 6 Mean ± 1 SE of the square root of mean carbon mass (g C m^{-2}) for different taxa in assemblage types 1, 2, and 3 (Figures 2, 3). Within taxa, bars that share the same symbol (filled or unfilled circle) or are linked by vertical lines do not differ (Tukey's studentized range tests on ranked data, $P < 0.05$)

fish predators, small snow crabs, and predatory Nemertean and Priapulid worms. The simulations indicated that these changes resulted mainly from the depletion of available energy during transfers through lower trophic levels when inputs of sediment OC were reduced.

The sediment OC pool integrates a range of factors associated with climate change, including: (i) the timing, duration, and extent of ice cover; (ii) the resulting magnitude and distribution of phytoplankton production; and (iii) the timing, strength, and direction of winds, which in turn affect temperature, ice cover, current flow, sediment grain size, the distribution of settled phytodetritus, and larval dispersal and settlement. Nevertheless, the response of benthic assemblages to

these variables via their indirect effects on sediment OC may at times be modified or overwhelmed by the strength of particular factors. For example, periods of exceptionally low or high temperatures, as result from persistent northerly or southerly winds, can alter the extent and timing of winter sea ice (Zhang, Woodgate, & Moritz, 2010). This factor in turn determines the annual extent of a summer cold pool of bottom water <2°C (Zhang, Woodgate, & Mangiameli, 2012), which can exclude a number of taxa. Contraction of the cold pool can allow invasions of important predators such as red king crab (*Paralithodes camtschaticus* Tilesius) or Pacific cod (*Gadus macrocephalus* Tilesius), which could have major effects on food-web structure and the

biomass of prey for endotherms. Moreover, population increases or altered distributions of important predators such as gray whales or walruses could impact benthic assemblages, as can chronic or catastrophic ice scour in shallower areas (Conlan & Kvitek, 2005; Coyle et al., 2007; Jay, Fischbach, & Kochnev, 2012; Oliver & Slattery, 1985; Oliver, Slattery, O'Connor, & Lowry, 1983). Effects of changing patterns of ice cover on access to the bottom or availability of resting platforms can also alter the viability of otherwise suitable benthic habitats for sea ducks and walruses (Jay et al., 2012; Lovvorn et al., 2014; Lovvorn, Rocha, et al., 2015). Nevertheless, our results indicate that sediment OC is an effective predictor of benthic assemblages over large areas of this region.

4.2 | Significance to endothermic predators

Benthic assemblage types associated with divergent levels of sediment OC have contrasting value to different endothermic predators. Eider ducks prefer mid-sized bivalves with shells of low to moderate thickness, which they swallow whole and crush in the gizzard (Lovvorn et al., 2003, 2014; Richman & Lovvorn, 2003). Accordingly, the higher biomass of Nuculana and Ennucula in assemblage type 1 corresponds to the greater use of the western region south of St. Lawrence Island by spectacled eiders during winter (Lovvorn et al., 2014). Walruses typically eat larger or thicker-shelled bivalves such as Serripes and Astarte without ingesting the shells (Born et al., 2003; Sheffield & Grebmeier, 2009). In the top 10 cm of sediments sampled by the van Veen grab, the latter bivalve taxa were common only in assemblage type 3. However in sandy nearshore sediments of the north-east Bering Sea, walruses excavated large individuals of the bivalve Mya truncata Linnaeus buried to a mean depth of 32 cm, the bivalve Macoma buried to a mean of 17 cm, and Serripes buried to a mean of 11 cm (Oliver et al., 1983). van Veen grabs such as ours do not sample these deeply buried bivalves, so evaluations of feeding habitat for walruses are incomplete (Beatty et al., 2016; Jay et al., 2014). Nevertheless, the presence of smaller (younger) bivalves near the sediment surface may indicate larger individuals buried deeper, and in the past, side-scan sonar detected extensive areas of walrus feeding furrows in what appear to have been type-3 habitats in the Chirikov Basin (Nelson & Johnson, 1987). Gray whales in this region feed mainly on amphipods (Brower et al., 2017; Oliver & Slattery, 1985). The amphipod biomass was greatest in assemblage type 3, corresponding to the traditionally heavy use of the Chirikov Basin by gray whales (Moore, Grebmeier, & Davies, 2003; Nelson & Johnson, 1987).

Starting in the late 1980s in the Chirikov Basin, benthic amphipods declined dramatically in gray whale feeding areas (Coyle et al., 2007). The amphipod decline was thought to result mainly from heavy feeding by the growing gray whale population; however, our results and the observed trends toward coarser sediment grain sizes and reduced sediment respiration rates (Moore et al., 2003) suggest that this shift also paralleled a decreased deposition of organic matter. Further reductions of sediment OC below the range we observed might bring about a transition to a sand dollar-dominated assemblage less suitable for foraging by endothermic predators (cf. Bluhm & Gradinger, 2008; Lovvorn et al., 2014). Assessing the inertia of such an assemblage to a reversion to a more profitable prey community (Clark & Johnston, 2009; van Nes, Amaro, Scheffer, & Duineveld,

2007) will require studies over time to observe the interactions of hydrography and assemblage structure.

4.3 | Value of predictive capability

Confidence in predicting changes in benthic assemblages from levels of sediment OC is tempered by the fact that the OC levels we observed generally corresponded to different geographic regions (Figure 1). These regions are expected to experience other important influences, such as proximity to and direction of major currents and sources of colonizing fauna. However, if further studies confirm the utility of sediment OC for inferring changes in benthic assemblages in this region, it could greatly enhance the information available for mapping, monitoring, and prioritizing the conservation of different habitats over time (Gonzalez-Mirelis & Buhl-Mortensen, 2015; McArthur et al., 2010; McHenry et al., 2017).

For example, farther north in the eastern Chukchi Sea, a critical migration corridor for endothermic benthivores (10–40 m in depth) extends along 500 km of coastline adjacent to areas recently considered for oil and gas development. Setting priorities for the placement of pipelines from offshore drill rigs to shoreline terminals, and for clean-up operations if a spill occurred, requires knowledge of the locations of high-quality, important habitats (Lovvorn, Rocha, et al., 2015; Schonberg et al., 2014). In particular, areas dominated by sand dollars thought to be poor foraging habitat for both endothermic and many ectothermic predators occupy a substantial fraction of the migration corridor (Feder et al., 1994); these areas should receive lower priority for protection than areas of high bivalve or amphipod density. Projecting the location, extent, and persistence of areas of dense benthic prey is important to long-term conservation efforts. This alongshore corridor is subject to quite variable and complex wind-driven currents (Danielson et al., 2017), and patchy dispersion of benthic assemblages and biomass. Thus, areas of high prey abundance are likely to shift around over time, perhaps with longer-term trends linked to the changing climate (cf. Lovvorn et al., 2014; Lovvorn, Rocha, et al., 2015). Unfortunately, over this large nearshore area, long-term, regular monitoring at adequate spatial resolution to indicate changes in patch structure for foraging birds and mammals is economically improbable. If periodic and perhaps opportunistic surveys of sediment OC can be used to infer important trajectories in the dispersion of benthic assemblages, more up-to-date information and longitudinal data for modelling would become available.

Moreover, if patterns of sediment OC can be predicted from wind-driven hydrography (cf. Danielson et al., 2012; Holt, Wakelin, Lowe, & Tinker, 2010; Myksvoll et al., 2012; Puls & Sundermann, 1990), and winds can be predicted by downscaling from climate models (Ådlandsvik, 2008; Najac, Lac, & Terray, 2011), there exists the possibility of projecting future changes in benthic assemblages from climate simulations (Weinert et al., 2016). A readily monitored variable such as sediment OC that integrates diverse physical and biotic processes, and that is central to trajectories of biomass and trophic interactions among species (Lovvorn et al., 2016), should facilitate the development of such capabilities. Total sediment OC has been mapped extensively throughout the Pacific Arctic and related to benthic biomass at large spatial scales that span different water masses

(Grebmeier et al., 2006, 2015). Such studies provide an important context for developing maps and predictions of more localized patch structure at smaller scales relevant to endotherms foraging in restricted areas of open water in winter and spring (cf. Lovvorn et al., 2014; Lovvorn, Rocha, et al., 2015). Although the resulting predictions of changes in habitat dispersion for endotherms will include appreciable uncertainty, estimates of the range and probability of alternative scenarios would be valuable for guiding the geographic focus of long-term planning efforts (Carroll et al., 2010; Hole et al., 2011). Given the importance of benthic communities to marine birds and mammals, subsistence hunters, fisheries, and biodiversity in general, developing such capabilities is an important goal.

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